PATTERNS OF FOLIAR PIGMENTATION IN BROMELIACEAE
AND THEIR ADAPTIVE SIGNIFICANCE[1]

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INTRODUCTION

Bromeliaceae has recently emerged as a major source of home, greenhouse and garden material. Chief among the aesthetic qualities responsible for this surge of horticultural popularity are the unusual growth habits and attractive patterns of leaf coloration characteristic of so many of its species. Most highly valued are taxa whose compact determinate shoots color up to bright hues of violet to red around the time of anthesis. Other widely cultivated populations exhibit variously cyanic leaves while in vegetative and reproductive phases. Yellow markings are present less frequently. These displays are usually heightened by exposure to intense sunlight.

The functional significance of anthocyanins in leaves has been the subject of much speculation and some investigation (e.g., Kerner & Oliver, 1895; Smith, 1909; Caldwell, 1971; Klein, 1978; Lee *et al.*, 1979), but so far Bromeliaceae has not figured in any of these considerations. Patterned albinism has been virtually ignored altogether. In this report, we describe the common foliar ornamentations occurring in the family and assign them to what impress us as functionally distinct categories. We also attempt to explain how a particular pigment display in conjunction with a specific shoot form may impart adaptive advantage in the field. Included is some empirical evidence to support several of these hypotheses.

THE PIGMENT CATEGORIES

Type 1. Ephemeral cyanic pigmentation associated with anthesis. Pigmentation of this description develops in recently expanded floral bracts and leaves as anthesis approaches. Anthocyanins accumulate in the cells of both epidermal layers. As in all other categories, tissues deeper in the leaf bear much less or no cyanic material.

Most often, only the youngest leaves immediately below the inflorescence are involved and then occasionally just the proximal blade area (e.g., *Neoregelia* spp.) or the distal portion (e.g., some *Tillandsia ionantha*). Sometimes the entire shoot responds (e.g., *T. brachycaulos*). Affected surfaces are typically expansive but can be scattered as smaller patches or more regularly arranged bands. In most, if not all, instances the appearance of anthocyanins is accompanied by a considerable diminution in the concentration of the underlying chlorophyll, leading to a much enhanced color display. At about the time the flowers wither, leaves again become concolorous (uniformly green) as chlorophylls reappear in the mesophyll and the anthocyanins fade.

The adaptive value of the Type 1 response is unequivocal. Most participating bromeliads are ornithophilous, a feature which requires that they become highly visible to birds at anthesis. Insect- and bat-serviced populations and those apparently relying on autogamous sexuality often lack this response as well as the cyanic floral bracts that figure prominently in the reproductive efforts of so many members of this family.

Type 2. Cyanic pigmentation associated with exposure. Bromeliads endemic to open sites – particularly at high altitudes -- frequently feature cyanic leaves. Upon relocation to a glasshouse or moderate to deep shade, they

become concolorous or at least fade to less extreme shades of red to purple. Exposure anthocyanins can occur in extensive patches and spots or uniformly over the entire blade surface. They are usually most highly concentrated in the adaxial surface. Unlike the first category, exposure pigmentation is a constant feature of the shoot regardless of its age or the season so long as the specimen remains in bright light.

Exposure coloration in other groups of plants is considered to be protective (Caldwell, 1971) and supposedly operates by shielding the delicate green mesophyll tissues from damaging near-UV and intense visible radiation. The disappearance of color in shade and its reappearance or intensification under fuller exposure support this contention. Type 2 pigmentation is dramatically illustrated by many atmospheric tillandsias and numerous epiphytic species of *Aechmea* and *Vriesea*, to cite just a small portion of the total.

Type 3. Leaf base pigmentation. Many tank and most bulbous atmospheric bromeliads posses deep purple, or tanniferous, leaf bases. The pigments responsible occur in both epidermal layers. Blades are concolorous or variously ornamented depending on the species.

Deposits of dark pigments deep in a rosulate shoot are not likely to screen harmful radiation nor are they apt to enhance photosynthesis. Cyanic leaf bases may, however, appreciably benefit cryptic wildlife whose survival is enhanced by a dark backdrop within the narrow confines of the tank microcosm. If these patterns are indeed advantageous to tank occupants, the investment will also benefit the plant. Impoundment bromeliads rely heavily, if not exclusively, on their tanks as sources of mineral nutrients (Benzing & Renfrow, 1971a, 1974). The more attractive and secure the leaf axils are to animal life, the more nutrients will be available for absorption. *Vriesea erythrodactylon* exemplifies this group (Figure 1).

Type 4. Abaxial cyanic pigmentation. Numerous bromeliads, some already identified in the field as shade-tolerant (Pittendrigh, 1948), feature a deep red abaxial epidermis but remain concolorous above. These taxa usually possess thin, sparsely trichomed leaves with relatively high fresh weight chlorophyll contents, low reflectance and low light compensation and saturation points (Benzing & Renfrow, 1971c).

Lee *et al.* (1979) have proposed that quite a few plants endemic to deeply shaded sites utilize the reflective properties of anthocyanins to enhance photoassimilation. Anthocyanins are particularly appropriate for this task since solar radiation is proportionally enriched in red light by selective absorption of the shorter wavelengths as it passes through leafy canopies (Federer & Tanner, 1966). A layer of red-reflecting material -- in this case represented by a cyanic abaxial epidermis -- is well placed in the leaves of numerous bromeliads to scatter unabsorbed red light back into the mesophyll where the chloroplasts have a second opportunity to utilize it. Examples are *Vriesea simplex*, *Aechmea fulgens* var. *discolor* and *Nidularium burchellii* (Figure 6).

Type 5. Permanent leaf variegation, spotting and fenestration. This group includes the most intriguing and varied pigment patterns in the family. It is also the most difficult to interpret. Several of the Type 5 pigment displays may enhance autotrophic performance, but under different exposure regimens. Others may impart as yet unspecified benefits. Subgroups comprising this complex category overlap considerably. In extreme expressions, they appear as follows:
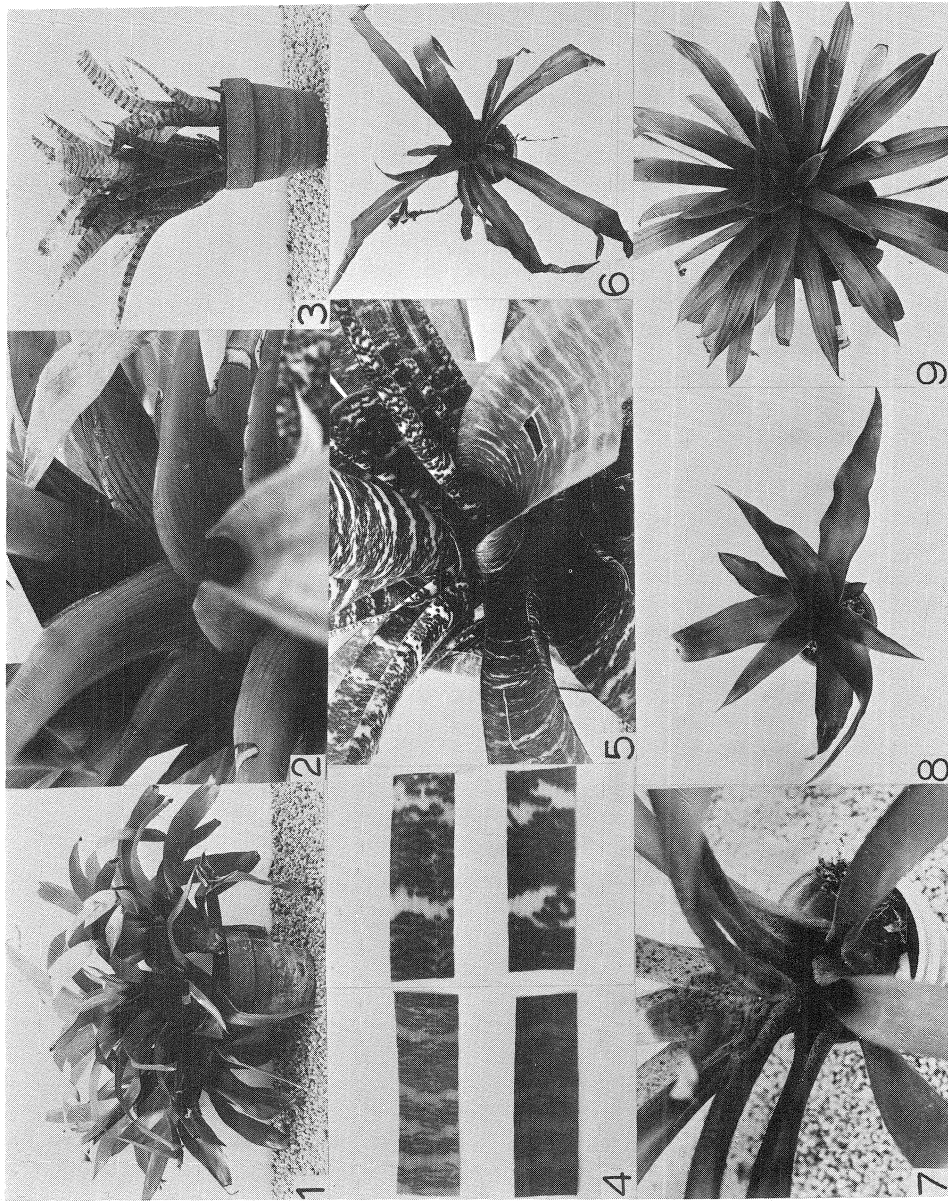
Figure 1. *Vriesea erythrodactylon* × 0.13. Figure 2. *Guzmania lingulata* × 0.38. Figure 3. *Neoregelia ampullacea* × 0.10. Figure 4. Distal blade sections of *Vriesea fosteriana*, left pair from older leaf, right pair from younger leaf. Figure 5. *Vriesea fosteriana* × 0.19. Figure 6. *Nidularium burchellii* × 0.13. Figure 6. *Vriesea regina* × 0.19. Figure 8. *Catopsis nutans* × 0.19. Figure 9. *Guzmania monostachya* × 0.19.

A. **Vertical cyanic pin stripes.** Individuals of this category are mesophytic tillandsioids with thin, broad, green leaves marked with narrow stripes of anthocyanin-laden epidermal cells extending from the base for various distances along the blade. Both adaxial and abaxial surfaces are usually involved -- e.g., *Guzmania lingulata* (Figure 2.).

B. **Broad horizontal cyanic stripes.** Dark markings on these species are much broader than the vertical ones and, as above, the intervening regions are concolorous. Horizontal stripes are often most distinct along the proximal portion of the leaf blade, but they usually continue with a more muted expression to the tip (*Vriesea splendens, V. glutinosa*). Anthocyanins are usually confined to the abaxial epidermis in members of Tillandsioideae, but may occur on both surfaces of the leaf among bromelioids. Additional examples are *Aechmea fosteriana* (Figure 11) and some populations of *Neoregelia ampullacea* (Figure 3).

C. **Cyanic spotting.** Pigmentation of this description consists of randomly scattered cyanic patches of variable size -- e.g., *Vriesea regina* (Figure 7). Affected cells are located in both epidermal layers. Pigmented regions may not correspond on both sides of the same leaf. Stripes and spots are sometimes combined in a single plant -- e.g., *Neoregelia* spp.

D. **Fenestration.** Anthocyanins are not always involved in this case. The leaf may simply be marked with sections -- often very regularly and finely distributed and shaped -- of chlorophyll-rich and more deficient areas. The fenestrae -- the relatively achlorophyllous "windows" -- are pale green to yellow or albino. They occur over much or all of the blade and are usually most accentuated toward the base. The fenestrations of tillandsioids are often separated by wavy or zigzag horizontal variegations of anthocyanic abaxial epidermis just below deep green mesophyll tissues that follow the same course (Figures 4, 5). Fenestrae occur with less spatial regularity on the leaves of member bromelioids, e.g., some clones of *Bilbergia saundersiana* (Figure 10). The more opaque zones between windows will hereafter be described as "shutters."

Vriesea fenestralis typifies subgroup D pigmentation where no cyanic tissues are involved. The deep green shutters of *Guzmania musaica* and *V. fosteriana* (Figures 4, 5) are backed with a cyanic epidermis.

Several other less commonly expressed or conspicuous pigment displays occurring in Bromeliaceae seem unsuited for assignment to any of the described categories. Among the most notable of these are the permanent bright pink to red fingernail markings of certain *Neoregelia* species involving only the distal few percent of the blade. We mention this and the occurrence of any other exceptions to underscore the incompleteness of the current taxonomy. As more is learned about bromeliad leaf ornamentation, additional categories and refinements within categories will be required.

BROMELIADS LACKING CYANIC DISPLAYS

Cyanic leaf displays are much more common in Bromelioideae and Tillandsioideae than in predominantly terrestrial Pitcairnioideae. Nevertheless, even among the first two subfamilies, whole taxa up to the genus may be exclusively or almost completely anthocyanin-free. *Catopsis* is perhaps the most noteworthy example. This group of about 35 ecologically diverse epiphytes produces white or yellow, sometimes fragrant, insect-pollinated flowers. Floral bracts are yellow to green. *Catopsis berteroniana*, an extreme heliophile, never develops a trace of Type 2 pigmentation in the most open exposures. Its leaves and those of several others with similar habitat preferences are covered with a waxy, highly reflective, cuticular powder that may provide protection against intense insolation in the absence of anthocyanins. *Catopsis sessiliflora* and *C. nutans*, both inhabitants of shady sites, bear little or none of the same material.
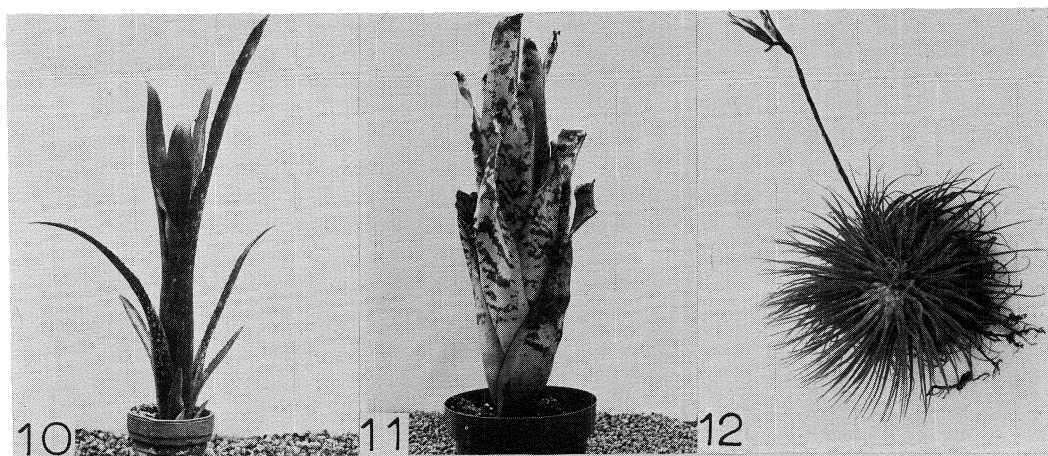
Figure 10. *Billbergia saundersiana* X 0.11. Figure 11. *Aechmea fosteriana* X 0.11. Figure 12. *Tillandsia argentea* X 0.43.

MATERIALS AND METHODS

All of the plants used in this survey were mature or nearly mature, greenhouse-cultured specimens. Patterns of CO_2 exchange were determined using an infrared gas analyser and procedures described previously (Benzing & Renfrow 1971b). A single, freshly harvested, leaf or portion of a leaf was used for each run. All runs were duplicated or triplicated. Chlorophyll determinations were made according to the procedures of Arnon (1949). Methods for establishing the elemental composition of leaf tissue were those employed in earlier investigations (Benzing & Seemann, 1978).

Leaf transparency to PAR (photosynthetically active radiation) was recorded with a Lambda Li-170 photometer. This was accomplished by placing the sensor directly under one or several overlapping leaves that had been pressed between two sheets of clean window glass. All readings were taken out of doors on clear days in late July and early August, 1979. Corrections were made for the small quantities of PAR that reflected upward and scattered laterally through the glass beneath a sample by subtracting values obtained directly below a strip of black tape about the same dimensions as the leaf samples.

RESULTS

Table I shows that shutters located in the distal portions of the upper (younger) mature leaves of *Vriesea fosteriana* (a Type 5-D pigmented species) contained higher concentrations of N, P, K, Mg and chlorophyll than adjacent fenestrae, while Ca, Fe, B, Mn, Cu, Zn and Mo were more evenly distributed between these two zones. Also, distributions of the same four macronutrients and chlorophyll were more uniform over comparable regions of older blades. Basal fenestrae (Figure 15) in leaves of all ages transmitted more PAR under intense illumination than distal windows (Figure 13). The opacity of the shutters was less distinct along appendages of all ages.

Compared on an equal surface area basis, the data in Table I shows that excised fenestrae from the upper leaf blades exhibited much weaker photosynthetic activity at light-saturating intensities (1600 $\mu E/m^2$-sec) than did adjacent shuttered zones. Windows and shutters from older blades performed

TABLE I: DATA PERTAINING TO THE STRUCTURE AND FUNCTION OF FOLIAR WINDOWS AND SHUTTERS IN *VRIESEA FOSTERIANA*.

POSITION IN ROSETTE	AREA	CHLOROPHYLL CONTENT (mg/cm² leaf surface)	MEAN ELEMENTAL CONTENT (PERCENT DRY WEIGHT)					MEAN ELEMENTAL CONTENT (PPM DRY WEIGHT)						MEAN MAXIMUM PHOTOSYNTHETIC RATE (mg CO_2/cm²·min)
			N	P	K	Ca	Mg	Mn	Fe	B	Cu	Zn	Mo	
Distal portion of upper leaf	Window	0.0089	1.13	0.09	1.08	0.22	0.11	14	95	19	7	21	1.00	14.6×10^{-5}
	Shutter	0.0442	1.58	0.13	1.32	0.22	0.14	12	86	20	8	22	1.09	41.3×10^{-5}
Distal portion of lower leaf	Window	0.0400	1.42	0.08	0.67	0.48	0.17	12	105	16	6	29	1.23	62.2×10^{-5}
	Shutter	0.0740	1.35	0.09	0.79	0.39	0.20	11	178	15	15	30	1.21	61.8×10^{-5}

more uniformly. Basal regions of old and young leaves that included both windows and shutters achieved some CO_2 consumption at very low intensities and photosaturated at about 400 $\mu E/m^2$-sec (Figure 16). Comparable distal sections exhibited a more sun-adapted photosynthetic response.

The fenestrae of younger blades of *Vriesea fosteriana* (Figure 13) and the entire leaf surfaces of *Guzmania lingulata* and *G. monostachya* were very transparent (Figure 14), probably in large part because of their relatively low chlorophyll content (Tables I, II). Several leaf layers of each guzmania were required to quench strong sunlight to the light compensation points of the respective taxa. Those of tubular *Billbergia saundersiana* (Figure 10) contained the smallest quantities of chlorophyll of all, but were still more opaque than *Guzmania monostachya*, probably because anthocyanins are abundant in both epidermal layers. Type 4 pigmented leaves of *Nidularium burchellii* were heavily chlorophyllous and the most opaque. Leaves with the highest chlorophyll levels tended to be the least transparent, but there were exceptions.

Additionally, Table II reveals that chlorophyll was much more concentrated in the distal shutters of *Guzmania musaica* and *Vriesea fenestralis* than in the fenestrae. The leaf bases were not examined. Windows and shutters were too closely placed to assay individually for transparency. Mature leaf blade samples containing both shutters and windows had fairly low light compensation and saturation points. *Catopsis nutans* and *Vriesea scalaris* leaves were moderately opaque (Figure 14) and both exhibited relatively high light compensation points. The former had a much higher light saturation point. *Billbergia* and *Nidularium*, being CAM genera, provided no photosynthetic responses measurable by CO_2 exchange phenomena.
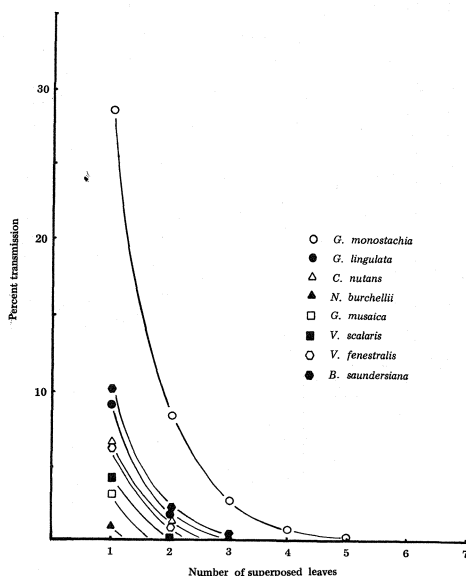
Figure 13. The transparency of various parts of a young mature leaf of *Vriesea fosteriana* under intense sunlight.
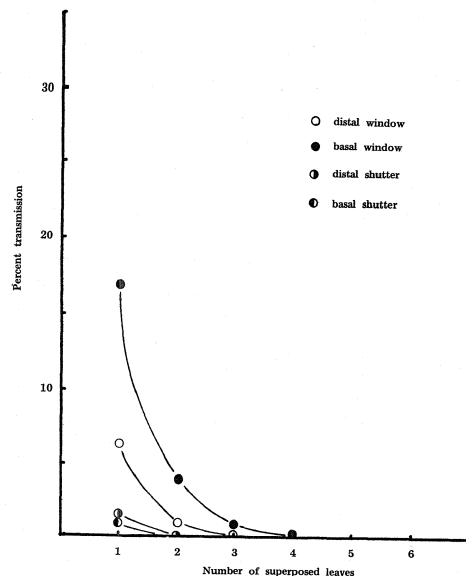

Figure 14. The transparency of the blades of mature leaves of various bromeliads under intense sunlight.

PHOTOSYNTHETIC PERFORMANCE AND ADAPTIVE TRADEOFFS

Under the best of circumstances, only a small fraction of the PAR impinging on a leaf will be used by that organ to fix CO_2. The rest is reflected, converted to heat or passed through the appendage unabsorbed. The proportions of incident PAR utilized for photoassimilation and variously lost by a particular leaf (an expression of its light use efficiency) will be influenced by many factors. Most important of the extrinsic ones is the strength and quality of the solar input. Direct intervention on the part of the plant to modify this factor at its source is, of course, impossible. Contrastingly, the transparency of an organ, its reflectivity, photosynthetic capacity, angle relative to the sun, juxtaposition to other leaves on the same plane, moisture status, stomatal resistance, boundary layer thickness, and so on, are all influenced by the organism to some degree (Gates, 1965; Woolley, 1971, Boardman, 1977).

Several authors (e.g., Horn, 1971; Brunig, 1976; Hallé *et al.* 1978; Fisher & Honda, 1979a, b) have pointed out that species-specific arrangements of leaves in the crowns of plants are adaptive -- particular configurations enhance carbon gain at particular light exposures and climatic regimens. According to Horn (1971, 1974), woody plants endemic to shaded habitats in mesic, temperate forests are likely to display their photosynthetic surfaces (leaves) in what amounts to a monolayer. In these instances, a canopy whose individual parts exhibit minimal effective overlap is most cost-efficient since little useful energy will penetrate beyond a deeper, more opaque barrier. Other species, preferring more exposed sites, intercept available PAR with a multilayered canopy. Here the substantial amounts of usable radiation that inevitably pass throught the uppermost layer of leaves can be utilized by more shade-adapted organs below.

So it seems that many of the factors affecting the capture and utilization of PAR by the individual leaf and the intact plant are under genetic con-

TABLE II: DATA PERTAINING TO THE STRUCTURE AND FUNCTION OF
MATURE BLADES (DISTAL PORTIONS) OF EIGHT TANK BROMELIADS

SPECIES	TYPE OF CANOPY	TYPE OF LEAF PIGMENTATION	MAXIMUM PHOTOSYNTHETIC RATE (mg CO_2/cm^2 -min)	APPROXIMATE LIGHT COMPENSATION POINT ($\mu E/m^2$ -sec)	APPROXIMATE LIGHT SATURATION POINT ($\mu E/m^2$ - sec)	TRANSPARENCY IN INTENSE SUNLIGHT OF ONE LEAF (% transmission)	CHLOROPHYLL CONTENT (mg/cm² leaf area)
Guzmania lingulata	multilayer	concolorous blade, Type 5-B leaf base	50.13×10^{-5}	15	400	9.3	0.030
Guzmania monostachia	multilayer	concolorous throughout	34.73×10^{-5}	60	400	28.0	0.022
Catopsis nutans	monolayer	concolorous throughout	45.06×10^{-5}	50	1000	6.6	0.042
Vriesea scalaris	monolayer	concolorous throughout	10.25×10^{-5}	65	250	3.7	0.040
Nidularium burchellii	monolayer	Type 4				1.2	0.091
Guzmania musaica	multilayer	Type 5-D throughout	49.28×10^{-5}	35	250	4.0	0.024 (window) 0.036 (shutter)
Vriesea fenestralis	multilayer	Type 5-D throughout	42.92×10^{-5}	25	400	7.2	0.041 (window) 0.070 (Shutter)
Billbergia saundersiana	tubular	Type 5?				10.3	0.017

trol and have been modified and brought into appropriate coincidence by Darwinian selection. "Appropriateness" is established by the environmental circumstances. These circumstances -- that is, the ecological context -- must be considered very broadly, however, if one is to understand why a particular pattern of form and display has been adopted. Conceivably, some patterns of foliar form and function have evolved with the primary impetus being the advantage of a heightened productivity under a particular exposure regimen. Analyses of these could be fairly straightforward. Interpretations of others -- those that were canalized along more restrictive pathways mandating major adaptive tradeoffs that have little direct association with photoassimilation but still impact heavily on that process -- will be more challenging.

THE MULTIPLICIOUS NATURE OF ADAPTATIONS

More than one service may be provided by a single adaptive character. Even the simplest features, such as the presence of a particular chemical compound in some part of the body, may provide two or more unrelated benefits to an organism, but one of these is apt to impart much greater advantage than the other(s), and thereby provide the major evolutionary impetus favoring the achievement of an ability to synthesize and accumulate that compound. Anthocyanins backing the shutters of many fenestrated bromeliads may be a case in point. Those in *Vriesea fosteriana*, in addition to providing a measure of photosynthetic enhancement on the same basis as that imparted by the Type 4 syndrome (but on a smaller scale), may also provide deterrent qualities and further protect the most expensively produced part of the plant against predators. Many phenolics have repellent or toxic effects on arthropods (McClure, 1975). Intuitively, of these two possible benefits, the influence on autotrophic performance seems least dispensable although that notion would be almost impossible to test empirically.

The same logic has even greater applicability to complex adaptations. Caswell *et al.* (1973), for instance, have suggested that the Kranz anatomy of
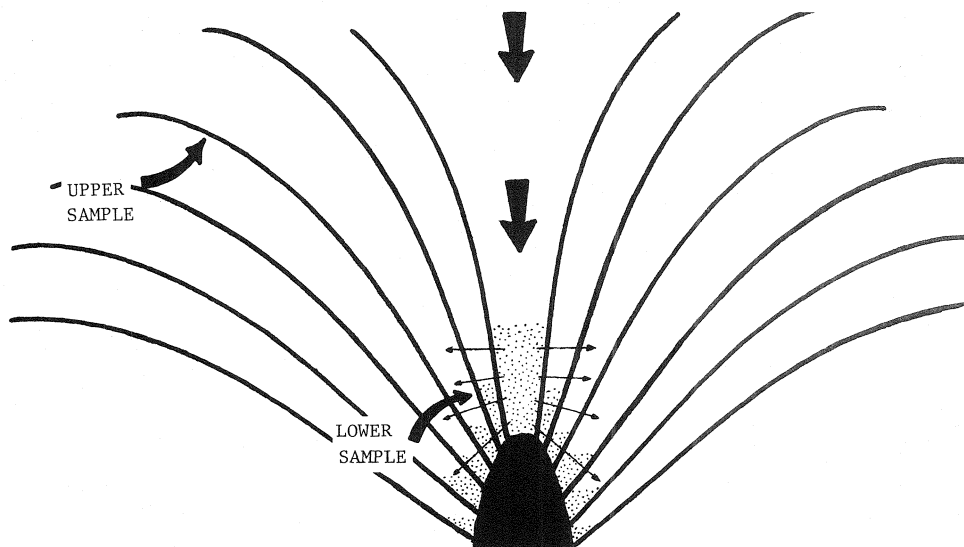

Figure 15. Diagram of the median section of a tank bromeliad (*Vriesea fosteriana*) leaf showing the excision sites for plant material assay. Also indicated is the light path striking the shoot from directly above. Stippled zones represent impounded moisture.

Hatch and Slack (C_4) species, in which disproportionally large amounts of nutrient-rich parenchyma are closely associated with the tough foliar veins, renders these species less appealing to phytophagous insects than otherwise similar C_3 types. In this instance, the low palatability of the C_4 appendage seems to be a fortuitous correlate of the Calvin-Benson carbon refixation scheme's location in bundle sheaths rather than in mesophyll cells. The advantages of a stronger immunity to insect attack probably had little to do with establishing the basic design of the C_4 leaf. Rather the need to separate the tandem carboxylating steps in space in order to facilitate the flow of carbon in these leaves determined their anatomy. Advantages accruing as a result of heightened photosynthetic rates and improved transpiration ratios (greater water use efficiencies) provided the necessary evolutionary impetus.

Incidentally, our results indicate that *Vriesea fosteriana* is not a conventional C_4 species (a CO_2 compensation point of 40-50 ppm was recorded). The heaviest concentrations of several nutrients do occur in narrow bands, although in this case across rather than along the parallel veins. Within these bands, the greatest depositions of chlorophyll as observed with a dissection microscope do, for some reason, occur around the vascular bundles.

CANOPY TYPES AMONG THE ROSULATE BROMELIADS AND THEIR EFFECT ON LIGHT HARVEST

1. **The monolayered rosette.** Excluding the lax shoots borne by various pitcairnioids, most of the rosulate bromeliads conform closely to one of four canopy displays. *Catopsis nutans*, an epiphytic shade-loving species with uniformly deep green, opaque leaves (Figure 8), tends to a monolayer, as does *Nidularium burchellii* (Figure 6) and various guzmanias, tillandsias, and
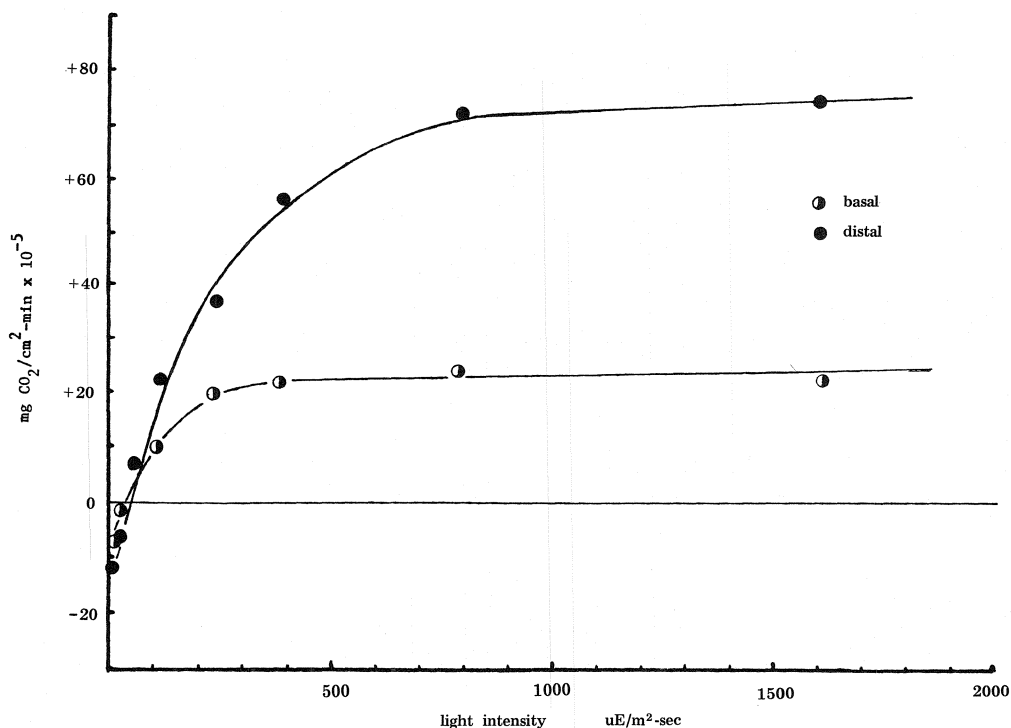

Figure 16. The photosynthetic response of basal and distal regions of the *Vriesea fosteriana* leaf to various light intensities.
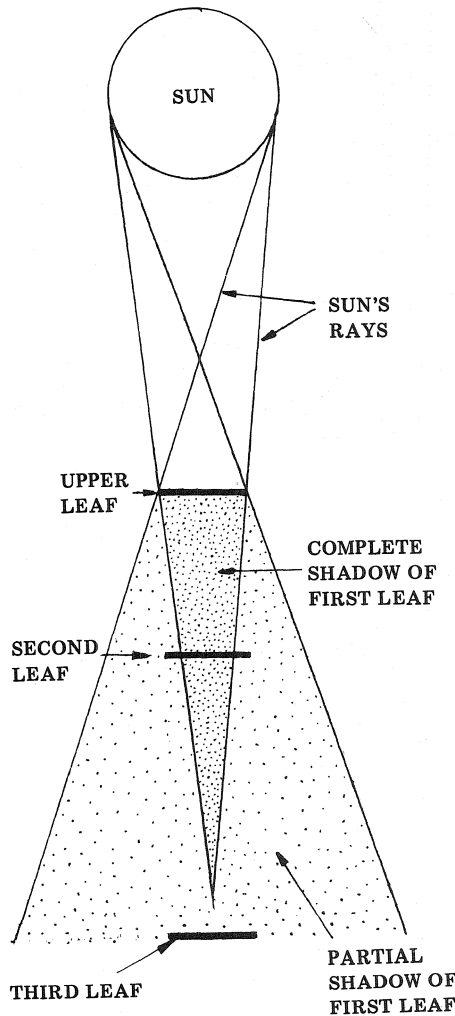
Figure 17. A schematic illustration des-
cribing shading phenomena among three
circular leaves of identical dimensions
variously positioned perpendicular to the
sun. The second leaf is close enough to
the upper leaf to be partially eclipsed by
that organ. The third leaf is displaced
far enough below the upper leaf to es-
cape that eclipse but not the indirect
shade cast by that leaf. The scales used
for distances and dimensions are obvi-
ously greatly exaggerated.

vrieseas with cyanic abaxial leaf sur-
faces. Many species of *Cryptanthus*, a
genus of small, low-growing, soft-
leaved plants, also appear to be good
candidates for this device. Among the
terrestrials, the monolayered display is
especially effective for a bromeliad
with such a low profile that its shoot
is exposed to very little illumination
from the sides and below.

2. The multilayered rosette. Form
modifications that adapt a majority of
bromeliads for impoundment -- a fea-
ture of special significance to their suc-
cess as epiphytes -- exacerbate the
problem of light harvest and could ex-
act a significant toll on photosynthetic
performance. Most mature tank-for-
mers have multilayered canopies, com-
prised of broad closely overlapped
leaves on a telescoped stem. Self-
shading is considerable (Figure 18).

The degree of shading of the sec-
ond leaf in a superposed series of two
on any plant is strongly influenced by
(1) the size and outline of the two
overlapping organs, (2) the distance
between them, (3) the distance be-
tween the upper leaf and the light
source, and (4) the size (width) of the
source (Horn, 1971; Figure 17). Since
the sun is so far away that its rays are
nearly parallel when they reach the
earth, factors (3) and (4) can be disre-
garded; variations in shading will be
determined only by the sizes and
shapes of the organs and the distances
between them. On a clear day, for ex-
ample, two superposed circular leaves
of equal area, perpendicular to the
sun's rays, must be displaced at least
50-70 times the minimum dimension
of the upper organ (in this case, the
diameter) to avoid direct shading of
the lower one. Under cloudy skies, or
under a host crown which acts as a
neutral density filter (light attenuator),
the distance needed between two leaves to eliminate all eclipsing of the
second by the first need be much less for the surface below to receive uni-
form (although weaker) radiation. Trees are much better designed to employ
the multilayered canopy than are short herbs since the vertical distance over
which leaves can be displayed is much greater on the longer shoot axis of the

former. It would not be surprising, therefore, to discover that certain qualities of foliar form, opacity and physiology among the multilayered bromeliads have been adapted to compensate for the dense packing of their canopy members.

3. The tubular rosette. Only in bright light is a dense tubular rosette consisting of a small number of vertical, tightly overlapped (poorly exposed) leaves apt to be feasible. *Billbergia saundersiana* (Figure 10) typifies this kind of shoot. Here, the tradeoffs obliged by the tank architecture seem to be especially heavy but, then again, the advantages of a deep central impoundment must be considerable under some circumstances, for instance, where the dry season is especially severe and prolonged. Perhaps a tubular rosette is not as much of a constraint on autotrophy as it seems. The lens effect of the tank could heighten the exposure of the inner leaves within the rosette considerably (Figure 15).

4. The ageotropic succulent rosette. As in the case of the tubular shoot, this growth habit is designed for high exposures. Many of these species, the "air plants," have few leaves or, if very numerous, the blades are narrow and terete (Figure 12). Their variously shaped and oriented, succulent and reflective rosettes have access to considerable lateral illumination. The several reasons why these plants exhibit low light use efficiencies will be discussed subsequently.

THE ADAPTIVE VALUE OF HETEROCHROMIC AND FENESTRATED LEAVES

The common occurrence of heterochromic leaf blades in Bromeliaceae is itself suggestive that the conventional, uniformly green appendage is not always the best device for a plant to employ as a light-capturing apparatus. Proposed reasons for Types 1, 2 and 3 pigmentation patterns are obvious and for the most part convincing. The role recently ascribed to the Type 4 scheme is also persuasive (Lee *et al.*, 1979). We suggest that the remaining category, at least the 5-D patterns as they occur among the tillandsioids, are devices for autotrophic enhancement although other functions are possible and in fact are likely concomitants.

The data in Table I illustrate that major chemical and physiological distinctions exist between the windows and shutters of a *Vriesea fosteriana* leaf. The task now is to determine why the shutters, occupying considerably less than the total leaf surface, are heavily committed to carbon gain while the remaining regions have little direct involvement in that same process. Why would a plant invest so much of its resources in foliar tissues that yield so little nutritional return?

1. To enhance nutrient economy. -- Epiphytes inhabit nutrient-deficient environments where several mineral elements are especially scarce (Benzing & Renfrow, 1971a; Benzing, 1978 a, b; Benzing & Davidson, 1979). This fact raises a question: Are any of the pigment patterns displayed by bromeliads in some way involved in a more economical use of these commodities? Most leaves exhibit an even distribution of photosynthetic machinery and associated CO_2 fixation capacity throughout the blade surface -- i.e., the entire leaf is a shutter. In comparison, a Type 5-D leaf may be relatively inexpensive to produce, especially in terms of N, one of the three elements known to limit the vigor of at least two vascular epiphytes (Benzing & Renfrow, 1971a; Benzing, 1978a; Benzing & Davidson, 1979). Were they constrained by the more conventional foliar design and shortages of certain key

elements, *Vriesea fosteriana* and its kind would have to rely on fewer or smaller leaves. In turn, a diminished leaf area would magnify the impact of injury and herbivory. Rather than producing small, more expensive and possibly more vulnerable appendages whose entire surfaces can harvest light, the Type 5-D bromeliad may be better served by larger, more robust, less vulnerable organs containing just patches of well-provisioned tissue.

2. To increase transport and diffusive capacity. -- Leaves of tank bromeliads no doubt fail to achieve a high light use efficiency in strong exposure for the same reasons that those of other plants do: insufficient vascular transport to move rapidly accumulating photosynthate to sinks; insufficient diffusive capacity to supply CO_2 to the chloroplasts; the light saturation of some stage of the photoassimilatory process itself. Perhaps some of these constraints are moderated by the interspersion of photosynthetically active tissues (the shutters) within an equally vascularized and porous (with the same density of stomata) but photosynthetically inert matrix (the fenestrae). These fenestrae could act in a service role, providing additional phloem transport capacity and CO_2 influx during periods of high exposure.

3. To refine the multilayer for light harvest. -- Whatever the benefits of concentrating the photosynthetic machinery in only a fraction of the leaf surface, the resulting transparent regions could yield at least one autotrophic advantage. The leaves of shade- and most sun-adapted bromeliads alike photosaturate at exposures well below those provided in sunflecks, which essentially represent beams of unfiltered sunlight and supply much of the usable PAR in shaded habitats (Benzing & Renfrow, 1971c; Björkman, 1973; Boardman, 1977). Less energy might be wasted in bright sun, whether intermittent or constant, by a compactly multilayered shoot if its leaves were differentiated into appropriately positioned transparent and photosynthetic zones. The presence of fenestrae could permit the use of much more of a heavy flux of PAR by a shoot whose leaves are so closely overlapped that their surfaces are strongly eclipsed by other appendages in the same canopy. Even if the presence of fenestrae diminished the light use efficiency of an upper layer of leaves below what it could be were those surfaces uniformly green, more of the total PAR impinging on that canopy might be harvested by the plant as a whole. Should this supposition obtain, the Type 5-D syndrome would not be cost-efficient to its multilayered bearers in very dimly lit habitats. Here the windows of the upper leaves would inevitably block some PAR which could have been converted to chemical energy had that radiation impinged on shutters. Under these circumstances, a uniformly green monolayer or possibly a more generally transparent multilayer (as will be discussed shortly) would be more effectively amortized. It seems that *V. fosteriana* and similar types may be best suited to live in moderate shade where sunflecks are common, or in more prolonged high exposures where the upper layers of the shoot are routinely operating at a low light use efficiency.

Type 5-D pigmentation may be most beneficial at the heavily shaded center of the shoot. Light entering this area comes exclusively from above through an aperture produced by a funnel of ascending young leaves. After striking the water column in the central interfoliar chamber, PAR, now proportionally enriched in the longer wavelengths, although somewhat diminished overall, is scattered against the containing leaf surfaces (Figure 15). Should bands of deeply cyanic epidermis be located on the abaxial surfaces of these organs (as is the case with *V. fosteriana*), they will be ideally posi-
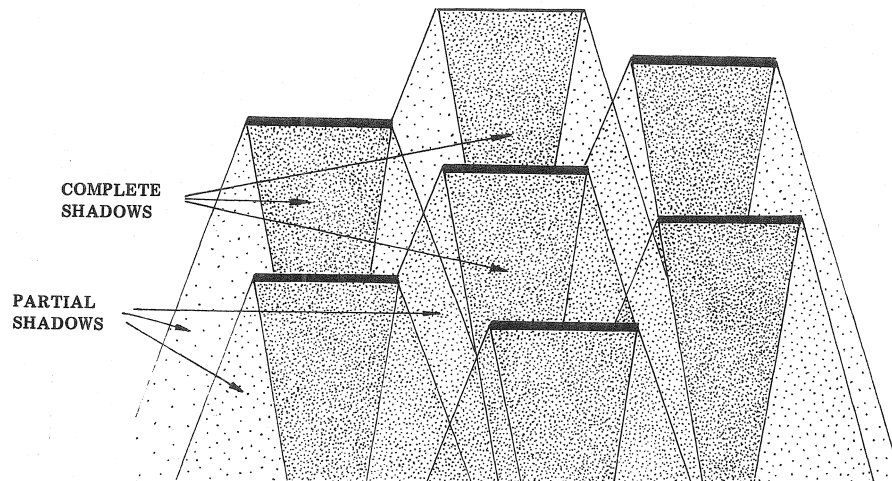
Figure 18. A schematic representation of a series of leaves positioned along one section of a bromeliad shoot. Complete and partial sun shadows are depicted to illustrate how the lower (older) leaves are deprived of radiant energy by those younger leaves above.

tioned to reflect unused red light back into the adjacent chlorenchyma facing the light source. PAR incident on the fenestrae located between these anthocyanin-backed shutters will be transmitted to older leaves aligned at most a centimeter or two distant.

The basal portions of *V. fosteriana* leaves (including shutters and almost pure white windows) do exhibit fairly low light compensation and saturation points, characteristics consistent with the theory that the dark, abaxial, cyanic layers of shutters located below deep green chlorenchyma tissue promote an efficient utilization of filtered dim light (Figure 16). As the leaf ages, its tip becomes progressively sun-adapted, judging from the responses of the distal vs. basal portions of mature leaves. Accompanying, and perhaps facilitating, this shift in functional profile of the tips is a partial greening of the fenestrae and fading of the cyanic backing -- plus an increase in the photosynthetic output at light saturation (Table I).

As intuitively appealing as this last of the three proposals may be, it raises an interesting question. Why, if the windows are designed to be little more than light-transmitting zones or inert areas rendering the leaf more expendable in case of predation or injury, aren't they more transparent to PAR? The rosette could achieve a higher light use efficiency in high exposures if they were. The leaves of some *Haworthia* and *Lithops*, for example, contain much clearer spots than those of any bromeliad; foliar tissues can be virtually transparent.

Mention should be made here that certain mesophytic tillandsioids with less elegantly pigmented leaves seem to be practicing a strategy which, in principle of operation, is similar to that just proposed for *V. fosteriana*. *Guzmania monostachia* (Figure 9) and *Vriesea erythrodactylon* (Figure 1), for example, feature shoots comprised of numerous congested, thin, uniformly green but very transparent, broad leaves. Several of those leaves must be overlapped to quench a beam of intense sunlight to a level below an individual organ's light compensation point (Figure 14; Table II). Thus some of the excess radiation that would otherwise be lost by a single leaf can be utilized by a succession of superposed photosynthetic surfaces borne on a single short axis.

CARBON FIXATION PATHWAYS VIS-À-VIS PIGMENTATION PATTERNS

The absence of Types 4 and 5 pigment schemes among the air plants is consistent with the notion that Type 4 exists to enhance light capture among monolayered species in shady habitats while Type 5 provides the same advantage to the multilayered model in brighter light. As mentioned previously, atmospherics conform to neither of these two shoot architectures and they are obliged by various xeromorphic features to inhabit exposed microsites in the forest canopy (Benzing & Renfrow, 1971c). Thus they do not need special pigmentation patterns to enhance light-capture; shading, whether self or environmentally imposed, is not a major problem.

Atmospherics inhabit dry, nutrient-deficient but sunny habitats where productivity is more likely to be limited by water deficits that reduce leaf porosity or by mineral insufficiencies than by inadequate exposure. The photosynthetic performance of the atmospheric leaf is additionally limited by the CAM mode of food manufacture itself. Under the best of environmental circumstances, when both water and minerals are abundant, the internal CO_2 supply governs the photoassimilatory activity of CAM succulents. As producers, CAM plants are unimpressive performers, to a great extent because of the modest quantities of CO_2 they can garner nonautotrophically during dark periods. One of the major limits on the dry weight accumulation of these plants, then, is the size of the carbon pool (as malic acid) acquired each night. Pool size is determined by several factors: the availability of sufficient stored carbohydrate to generate energy and PEP (phosphoenol pyruvate); PEP carboxylase activity; atmospheric CO_2 supply; and, ultimately, the volume of the vacuolar area for malate storage. Some additional CO_2 may be fixed autotrophically, but among the air plants at least, this quantity is likely to be modest (Benzing & Renfrow 1971b). Therefore, atmospherics probably intercept much more PAR than they need to convert all of the available CO_2 to sugar during a photoperiod. Indeed, the pronounced light-scattering qualities of the highly evolved tillandsioid foliar trichome suggest that the plant must dissipate excess light rather than absorb all that falls on the shoot. In any case, a plant receiving more than enough energy to deal with its supply of inorganic carbon would not be expected to evolve characteristics whose primary reason for being was to enhance the capture and utilization of PAR to photoassimilate that carbon.

Compared to CAM types, nonstressed, mesomorphic C_3 leaves have a more open-ended potential to utilize large quantities of PAR. It may be no coincidence that the most striking Type 5-D pigment patterns, those featuring the least opaque windows and deepest green shutters backed by an abaxial cyanic epidermis, are found among the mesophytic tillandsioids rather than the similarly constructed tank bromelioids which practice the less productive mode of carbon fixation. Five-D pigment displays may serve a different purpose in Bromelioideae -- perhaps blocking excess light in their exposed habitats.

Light probably does limit the productivity of some bromelioids in very dimly lit sites, however. The presence of the Type 4 pigment scheme in *Aechmea fulgens* var. *discolor* and *Nidularium bruchellii* seem to bear this out. In making this statement, we are assuming, of course, that these relatively mesic bromeliads are, in fact, obligate CAM types which, as members of Bromelioideae, they are supposed to be (Coutinho, 1965, 1969; McWilliams, 1970). Both species might prove to be intermittent CAM practitioners capable of switching to the more productive mode of photosynthesis during the rainy

season when low water use efficiency can be tolerated.

FIELD TESTS OF THE PROPOSED HYPOTHESES

Extensive research will be required to test all of these hypotheses and suggestions and to refine further and expand the pigmentation categories. We have purposely overlooked a number of potentially confounding physiological considerations to cast them in this first rudimentary form. In the meantime, circumstantial support of, or refutation for, the basic ideas presented and reviewed in this paper may be sought in the field by noting the habitat preferences of various bromeliads, their growth forms and leaf characteristics. According to the logic presented to explain the adaptive values of Types 1-5 pigmentation displays, a number of correlates should be found. Among these are:

1. Rosettes of red-backed leaves should display minimum leaf overlap (tend toward a monolayer) and should be found growing in very deep shade, perhaps close to the ground surface if terrestrial. Their chlorophyll content should be relatively high.

2. Species whose shoots bear fenestrated, banded, spotted or variegated leaves will likely be densely multilayered and prefer moderate to higher exposure rather than very deep shade.

3. Species with multilayered canopies routinely encountered in fairly deep shade should have very transparent, uniformly green leaves. Species of this description will probably not prefer the darkest sites inhabited by bromeliads.

4. Anthocyanin development in the adaxial epidermis should occur in specimens exposed to strong illumination.

5. Plants with dark leaf bases are likely to be those whose shoots are borne singly and exposed rather than as compact clusters or obscured by persistent dead leaves.

6. Specimens with tubular rosettes comprised of thick, opaque leaves should prefer high exposure and inhabit regions with a pronounced dry season.

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